

# TAXONOMIC IMPLICATIONS OF BIGNONIACEAE PALYNOLOGY<sup>1,2</sup>

ALWYN H. GENTRY<sup>3</sup> AND A. SPENCER TOMB<sup>4</sup>

## ABSTRACT

The neotropical genera of Bignoniaceae are surveyed palynologically and applications of palynology to the taxonomy of the family are reviewed. The family is markedly eurypalynous and pollen morphology is extremely useful taxonomically in generic delimitation. However, most of the divergent pollen types found in the family appear to have evolved independently in different lineages, limiting the applicability of palynological data to tribal and familial classification. The importance of interpreting palynological data in taxonomic context is emphasized. Several generic realignments and informal subtribal groups are proposed based largely on palynological evidence.

Genera of Bignoniaceae are notoriously difficult to recognize (Lawrence, 1951; Gentry, 1973). This has largely been due to taxonomic over-splitting. In fact, there are fewer species per genus in Bignoniaceae than in any other large or medium-sized plant family (Gentry, 1973) and Willis's *Dictionary* (Airy Shaw, 1966) lists 54 monotypic genera. Critical redefinition of genera is clearly the major taxonomic problem in the family. The careful use of pollen morphology has been a valuable tool in generic delimitation and in understanding relationships in the family.

The Bignoniaceae are conspicuously eurypalynous (Buurman, 1977; Tomb & Gentry, in prep.), despite Rendle's (1925) statement to the contrary. Figures 1–9 demonstrate some of the pollen diversity of the family. The taxonomic potential of pollen morphology in Bignoniaceae has long been appreciated, and Urban's (1916) early palynological study of Bignoniaceae is a classic. Pichon (1945), Gomes (1955) and other subsequent workers followed Urban's lead in proposing numerous new genera based on palynological differences. Unfortunately, the lack of any overall understanding of the family has led to repeated taxonomic misinterpretations.

Previous studies of the pollen of this family have relied mostly on light microscopy and some of the misinterpretations of pollen morphology are due to the difficulties of light microscopic analysis. Even though several recent papers on bignon pollen have been based largely on SEM work and have provided taxonomically important new information (Ferguson & Santisuk, 1973; Buurman, 1977), no attempt has yet been made to apply electron microscopic data to the taxonomy of more than a limited representation of the family. Moreover, even some recent workers with Bignoniaceae pollen have misinterpreted taxonomic and palynologic relationships in the family. Thus Mitra (1968) concluded that the family must be polyphyletic on account of its great palynological diversity and the presence of both putatively primitive and advanced pollen types. Suryakanta (1973) emphasized the essential palynological cohesiveness of the family but sug-

<sup>1</sup> Supported in part by NSF grant GB 40103.

<sup>2</sup> Contribution No. 80-191-A from the division of Biology and Kansas Agricultural Experiment Station.

<sup>3</sup> Missouri Botanical Garden, Post Office Box 299, St. Louis, Missouri 63166.

<sup>4</sup> Department of Biology, Kansas State University, Manhattan, Kansas 66502.



gested an unlikely derivation of Bignoniaceae pollen types from a spiroaperturate ancestral form. Most of these recent studies, even Buurman's (1977) excellent contribution, have been marred by taxonomic errors when dealing with the difficult neotropical taxa.

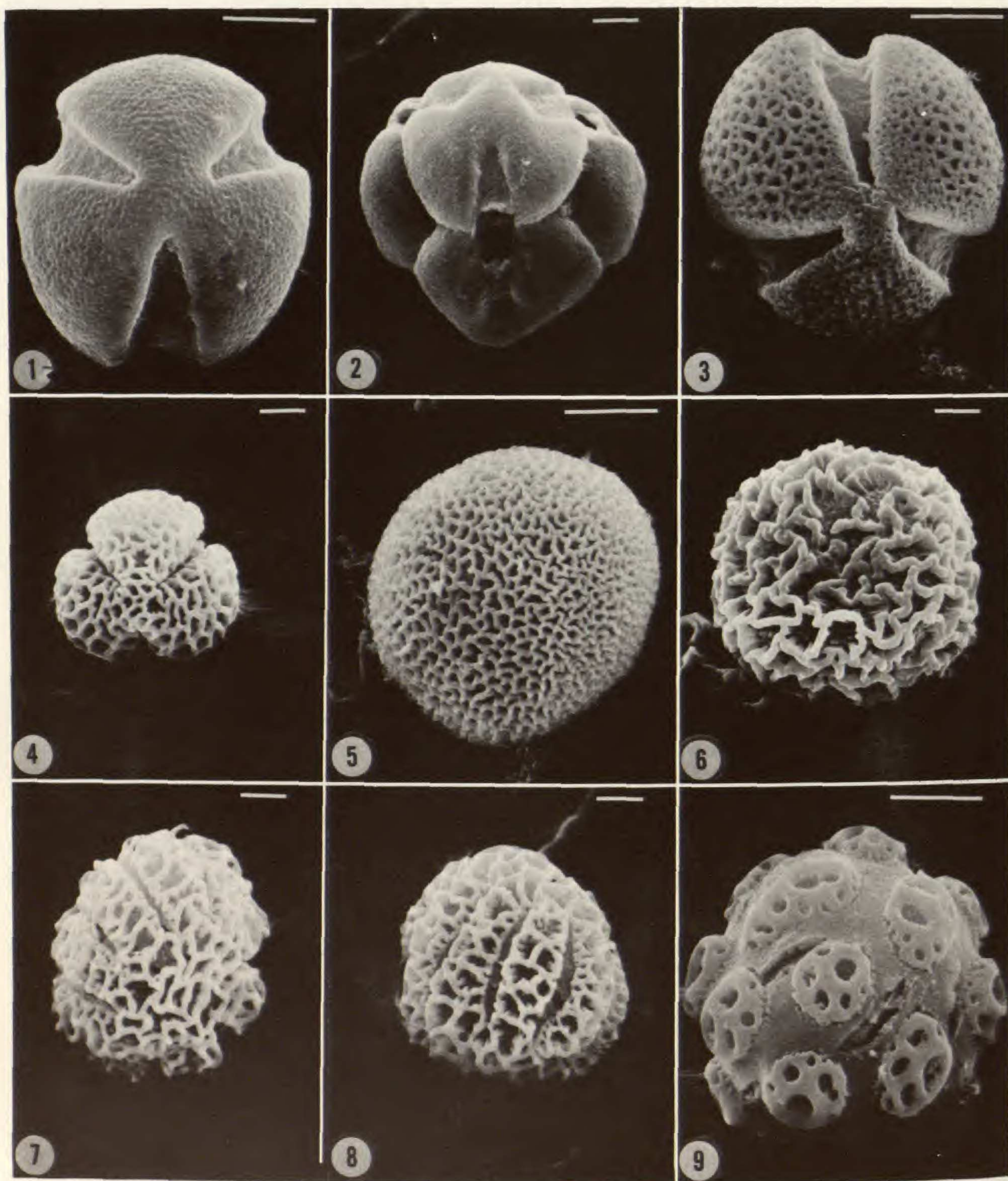
One major problem which has plagued the interpretation of Bignoniaceae is a conspicuous lack of taxonomic perspective on the part of students of its palynology. Thus, when a palynologist discovered a palynologically atypical species in one genus, it was frequently segregated as a new genus; however, most such species had been erroneously assigned in the first place and could have been reassigned to some other established genus with which they agree both palynologically and morphologically. Such segregate genera as *Blepharitheca* (from *Saldanhaea* but better assigned to *Cuspidaria*, Gentry, 1973), *Nestoria* (from *Memora* but better assigned to *Pleonotoma* (Gentry, 1976c), and *Orthotheca* (see the following paper), provide clear examples.

Another important point made obvious by the present study is that pollen can vary intragenerically as does morphology. Pollen should not be accorded the disproportionate emphasis in generic delimitation which has characterized previous palynological work in the family (Pichon, 1945; Mitra, 1968). On the other hand, palynological variation cannot be ignored, as has been the inclination of traditional taxonomists (Bureau & Schumann 1896–1897; Standley & Williams, 1974). Palynological characters must be evaluated in taxonomic context as one of many potentially significant indicators of evolutionary and systematic relationships.

*Crescentia* provides a good example of the taxonomic pitfalls of palynological over-reliance. There are two Central American species—*C. alata* with mostly 3-foliolate leaves, and *C. cujete* with simple leaves. These species are so closely related that occasional simple-leaved variants of *C. alata* cannot be separated with certainty from *C. cujete*. The two apparently hybridize in nature and a challenge to the validity of their *specific* segregation would be on stronger grounds than an attempt to separate them generically. However, several palynologically oriented authors have contrasted the 3-colpate pollen of *C. alata* with the (supposedly) inaperturate (Urban, 1916) or multiporate (Mitra, 1968) pollen of *C. cujete* and concluded that these two species constitute separate genera. *Crescentia alata* is either called *Pteromiscus* or, worse, placed in distantly related *Parmentiera* with which it has almost nothing in common except shared tribal and familial characteristics and the 3-colpate pollen. The SEM emphasizes the palynological similarity of *C. cujete* and *C. alata*. The dimensions and exine sculpturing of both species are similar. The main difference is in the number and size of colpi which the SEM reveals to have been misinterpreted. The six colpi of *C. cujete* are each half as long as one of the three colpi of *C. alata* and oriented in the same position. Almost certainly each of the long colpi of *C. alata* has become evolutionarily separated equatorially into two smaller colpi, a relatively minor change clearly unworthy of generic segregation in the absence of any additional evidence.

*Anemopaegma* provides a similar example. Urban (1916) characterized the genus as inaperturate, based on his light microscopic study. In fact, the type species of the genus, *A. arvense* (examined by Urban under the name *A. mirandum*) proves to have perisyncolpate pollen with the higher resolution of the





FIGURES 1-9. Main pollen types of neotropical Bignoniaceae.—1. *Xylophragma seemannianum*, tricolpate, psilate-foveolate, polar view.—2. *Cuspidaria floribunda*, psilate-foveolate tetrad.—3. *Pyrostegia dichotoma*, tricolpate, finely reticulate, subpolar view.—4. *Martinella obovata*, tricolpate, coarse-reticulate, polar view.—5. *Cydista aequinoctialis*, inaperturate, medium-reticulate.—6. *Distictella magnoliifolia*, inaperturate, coarse-reticulate.—7. *Amphilophium paniculatum*, stephanocolpate, coarse-reticulate, subpolar view.—8. *Amphilophium paniculatum*, stephanocolpate, coarse-reticulate, equatorial view.—9. *Sparattosperma leucanthum*, areolate. Lines in all figures equal 10  $\mu$ m.

SEM. Most other *Anemopaegma* species are also perisyncolpate, although a few are stephanocolpate. Thus segregation of the colpate species as *Pseudopaegma* is unjustified, even palynologically. These two genera are identical in all other characters and should be merged as has already been suggested (Gentry, 1976c).



An overview of tribal divisions of Bignoniaceae provides the necessary perspective for evaluation of the palynological evidence. The Bignoniaceae are predominantly neotropical (600 out of 800 species) and most of its tribes also are restricted to the New World. The largest tribe, Bignonieae, has 349 species and is entirely neotropical except for one species in the southeastern United States. All genera are exclusively or predominantly tendrillate vines, have anomalous wood anatomy (with radially arranged phloem arms in cross-section), and have fruit dehiscence parallel to the septum. The six species of Old World trees and nontendrillate climbers (*Oroxylum*, *Hieris*, *Nyctocalos*, *Millingtonia*), which are traditionally included here, are probably not closely related to the New World genera and better placed in a separate tribe Oroxyleae (Gentry, 1979b). The second major tribe, Tecomeae, is pantropical in distribution and also includes a few temperate zone genera. Its members are mostly trees and shrubs but also include a few nontendrillate vines which lack anomalous wood anatomy; fruit dehiscence is perpendicular to the septum. Two tribes which are usually lumped together have indehiscent fruits. Crescentieae in the narrow sense (Gentry, 1979b) includes three genera and 33 species of trees and shrubs, mostly in Central America and the West Indies; it is characterized by indehiscent fruits and bat-pollinated flowers. The indehiscent-fruited Madagascar Bignoniaceae (plus *Kigelia* of continental Africa) are independently derived from a different Tecomeae stock and should be treated taxonomically as the tribe Coleeae (Gentry, 1976b). Three neotropical genera (*Schlegelia*, *Gibsoniothamnus*, and *Synopsis*) of simple-leaved lianas and shrubs, which are usually hemiepiphytic and have berrylike indehiscent fruits, have traditionally been included in Crescentieae. They merit tribal recognition as Schlegelieae and may be closer to the Scrophulariaceae. Finally, two small neotropical genera are usually recognized as monogeneric tribes—Eccremocarpeae with six species in the Andes and Tourrettieae with one species in the Andes and upland Central America. *Eccremocarpus* is a wiry vine with multifoliolate, usually tripinnatisect tendrillate leaves, tubular hummingbird-pollinated flowers, a 1-celled ovary with parietal placentation and a thin-walled ovoid capsule without a septum. *Tourrettia* is an annual herbaceous vine with tendrillate leaves, a 4-loculed ovary, and spiny burlike incompletely dehiscent epizooic fruit. On the basis of morphology, these eight tribes are clearly natural.

The following paragraphs and Table 1 summarize Bignoniaceae palynological types by tribe and genus with different taxonomic assemblages which share a given pollen type indicated. Descriptions of Bignoniaceae pollen types and palynological interpretations have been emphasized in Tomb & Gentry (in prep.) and Buurman (1977). This paper focuses on the systematic utility of Bignoniaceae pollen. The major purpose of this paper is to demonstrate the utility of palynological data in generic and subtribal realignment of the neotropical Bignoniaceae. The following paper in this issue (Gentry, 1979c) formally makes some of these realignments. Species examined for this study are listed in the Appendix.

#### TECOMEAE

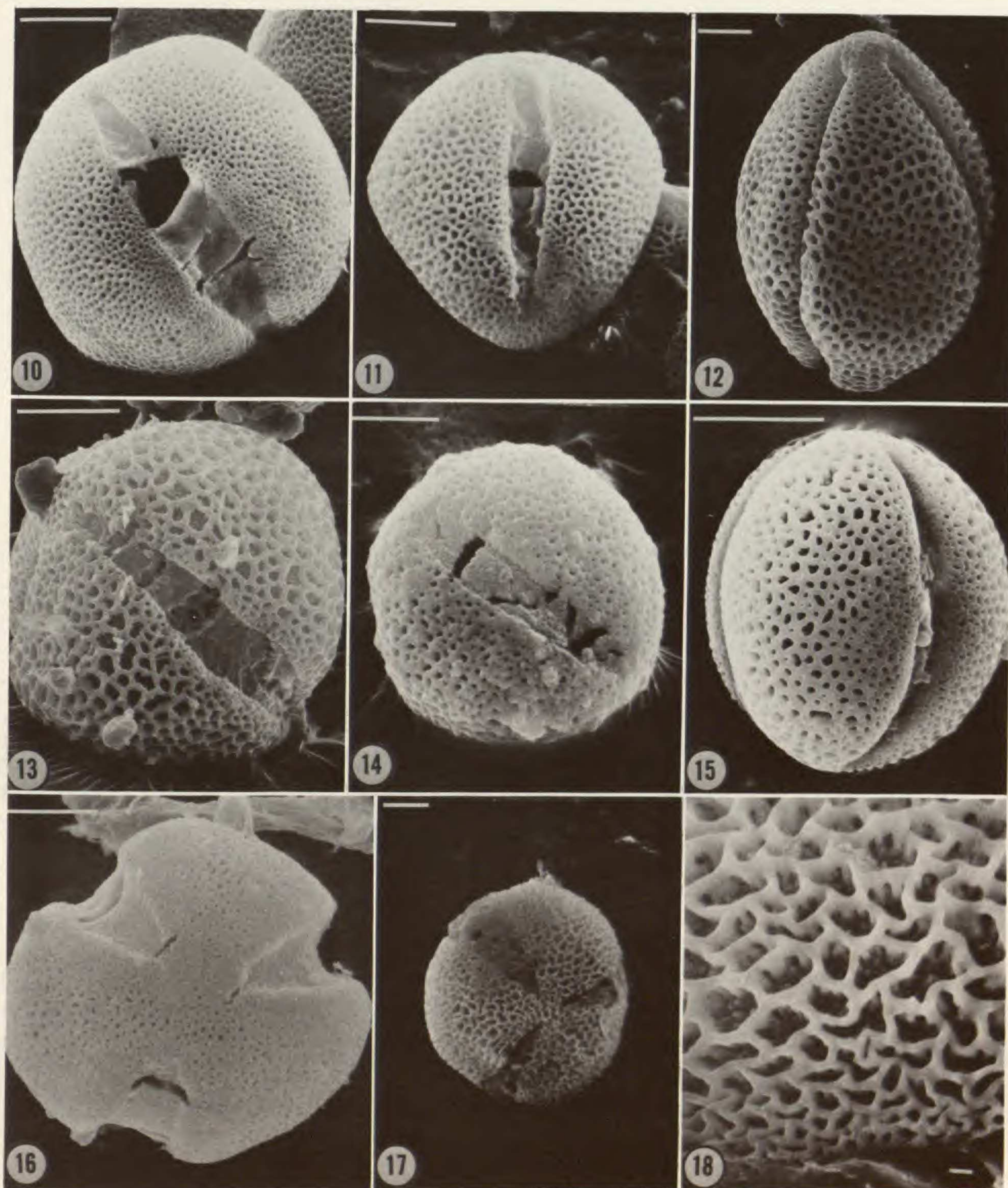
Genera of the less-specialized tribe Tecomeae are relatively well defined, both morphologically and palynologically. There are only three fundamental pollen



TABLE 1. New World Bignoniaceae pollen types.

Pollen Type	Genera
Psilate and microperforate, 3-colpate (4–6-colpate in <i>Leucocalanthe</i> )	BIGNONIEAE: <i>Arrabidaea</i> , <i>Ceratophytum</i> , <i>Dolichandra</i> , <i>Fridericia</i> , <i>Leucocalanthe</i> , <i>Macfadyena</i> , <i>Manaosella</i> , <i>Melloa</i> , <i>Parabignonia</i> , <i>Paragonia</i> , <i>Paradolichandra</i> , <i>Periarrabidaea</i> , <i>Pseudocatalpa</i> , <i>Setilobus</i> , <i>Spathicalyx</i> , <i>Xylophragma</i> TECOMEAE: <i>Digomphia</i> , <i>Jacaranda</i> ECCREMOCARPEAE: <i>Eccremocarpus</i> TOURRETTIEAE: <i>Tourrettia</i>
Psilate, 3-colpate tetrads or polyads	<i>Cuspidaria</i>
Finely reticulate, 3-colpate (to 4-colpate in <i>Pyrostegia venusta</i> and <i>Roentgenia</i> )	BIGNONIEAE: <i>Callichlamys</i> , <i>Lundia</i> , <i>Mussatia</i> , <i>Pachyptera</i> (except <i>P. alliacea</i> ), <i>Piriadacus</i> , <i>Pleonotoma</i> , <i>Pyrostegia</i> , <i>Potomoganos</i> , <i>Stizophyllum</i> , <i>Tanaecium</i> (except <i>T. apiculatum</i> and <i>T. nocturnum</i> ), <i>Roentgenia</i> (reticulum somewhat spinulose). TECOMEAE: <i>Argylia</i> , <i>Cybistax</i> , <i>Godmania</i> , <i>Campsis</i> , <i>Campsidium</i> , <i>Paratecoma</i> , <i>Tabebuia</i> , <i>Tecoma</i> , <i>Zeyheria</i> (also all Old World genera except some species of <i>Incarvillea</i> and <i>Stereospermum</i> ) CRESCENTIEAE: <i>Parmentiera</i> , <i>Crescentia alata</i> SCHLEGELIEAE: <i>Schlegelia</i> (large-flowered species)
Areolate/perisyncolpate	BIGNONIEAE: <i>Gardnerodoxa</i> , <i>Mansoa</i> (s.s.), <i>Memora flavida</i> , <i>M. pedunculata</i> , <i>M. cristicalyx</i> , <i>M. imperatoris-maximiliani</i> TECOMEAE: <i>Delostoma</i> , <i>Perianthomega</i> , <i>Sparattosperma</i>
Areolate tetrads	<i>Catalpa</i> , <i>Chilopsis</i>
Inaperturate, medium-reticulate	BIGNONIEAE: <i>Clytostoma binatum</i> , <i>C. pterocalyx</i> , <i>Cydista aequinoctialis</i> (mostly), <i>C. potosina</i> , <i>Phryganocydia</i>
Inaperturate, coarse-reticulate	BIGNONIEAE: <i>Adenocalymma</i> , <i>Distictella</i> , <i>Distictis</i> , <i>Memora</i> (except <i>M. flavida</i> group), <i>Pithecoctenium</i> , <i>Tanaecium apiculatum</i> , <i>Clytostoma costatum</i> , <i>C. sciuripabulum</i> , <i>C. uleanum</i> , <i>C. convolvuloides</i> (interrupted exine)
Stephanocolpate (zonocolpate), coarse-reticulate	BIGNONIEAE: <i>Amphilophium</i> , <i>Anemopaegma robustum</i> , <i>A. insculptum</i> , <i>Glaziovina</i> , <i>Haplolophium</i> , <i>Urbanolophium</i> .
3-colpate, coarse-reticulate	<i>Martinella</i>
Polyporate, finely reticulate	<i>Amphitecna</i>
Polyporate, coarse-reticulate	<i>Tanaecium nocturnum</i>
Spiroaperturate	<i>Neojobertia</i>
Pericolpate (pantocolpate)	<i>Anemopaegma</i> (mostly), <i>Cydista decorum</i> , <i>C. lilacina</i> , <i>C. diversifolia</i> , <i>C. aequinoctialis</i> (in part), <i>Pachyptera alliacea</i>
Spinulose, inaperturate	<i>Cydista heterophylla</i> (several unrelated species of other genera— <i>Phryganocydia</i> , <i>Roentgenia</i> , <i>Adenocalymma</i> , <i>Cyclostoma</i> , <i>Memora</i> —also show tendency in this direction)
Polyporate, complex exine patterns	<i>Macranthisiphon</i> , <i>Saritaea</i>
Ecolpate, 3-porate	<i>Schlegelia</i> (small-flowered species)
Not examined: <i>Romeroa</i> , <i>Ekmanianthe</i> , <i>Synapsis</i> .	





FIGURES 10-18. Tricolpate, finely reticulate Bignoniaceae pollen.—10. *Tabebuia rigida* (Tecomeae), equatorial view.—11. *Spathodea campanulata* (Tecomeae), equatorial view.—12. *Oroxylum indicum* (Oroxyleae), subequatorial view.—13. *Pachyptera standleyi* (Bignoniaceae), equatorial view.—14. *Parmentiera macrophylla* (Crescentieae), equatorial view.—15. *Ophiocolea floribunda* (Coleaeae), equatorial view.—16. *Argylia robusta* (Tecomeae), polar view.—17. *Pachyptera parvifolia* (Bignoniaceae), polar view.—18. *Pachyptera parvifolia* (Bignoniaceae), exine closeup. Lines in all figures, except Fig. 18, equal 10  $\mu\text{m}$ . Line in Fig. 18 equals 1  $\mu\text{m}$ .

types in New World Tecomeae; two additional types occur in Old World species of Tecomeae, inaperturate (or monocolpate?) in two species of *Stereospermum* (Ferguson & Santisuk, 1973) and stephanocolpate and subspinulose in *Incarvillea* (Fig. 21).



## 3-COLPATE, FINELY RETICULATE

This is the most widespread pollen type in Bignoniaceae and in Tecomeae. Nearly all the Old World species have 3-colpate, finely reticulate pollen (e.g., *Spathodea*, Fig. 11) and have been studied in detail by Buurman (1977). The largest neotropical genus, *Tabebuia*, also has 3-colpate, finely reticulate pollen (Fig. 10). The uniformity of pollen in morphologically heterogeneous *Tabebuia* supports its retention as a single genus and argues against persistent attempts (e.g., Mattos, 1970) to segregate simple-leaved from palmately compound-leaved species or the species with irregularly ridged capsules (*Roseodendron*) from the ones with smooth capsules. Even segregate genera adequately justified on other grounds—*Godmania*, *Paratecoma*, *Zeyhera* and *Cybistax*—are palynologically indistinguishable. *Tecoma*, mostly Andean and with pinnately compound leaves, has similar pollen, as do north-temperate *Campsis*, south-temperate *Campsidium*, and all Old World genera, except some species of *Stereospermum* and *Incarvillea*. *Astianthus*, traditionally but erroneously placed in Bignoniaceae, also goes here. *Argylia*, the herbaceous genus of the southern Andes has this type of pollen (Fig. 16), although the colpi of some species are operculate with the pollen thus appearing 6-geminicolpate (see also Gleisner & Ricardi, 1969). The pollen of *Argylia* is thus quite unlike that of *Incarvillea* (Fig. 21), the herbaceous Himalayan genus with which it is often compared, and suggests that these two genera (and their sometimes segregates *Oxymitus*, *Amphicome*, and *Niedzwedskia*) represent convergence rather than a phytogeographical conundrum. Buurman (1977), whose main focus was on this pollen type, recognized five subtypes based on lumina index (ratio of equatorial to polar lumina diameters); we find this character intragenerically variable and of little taxonomic significance at the generic level.

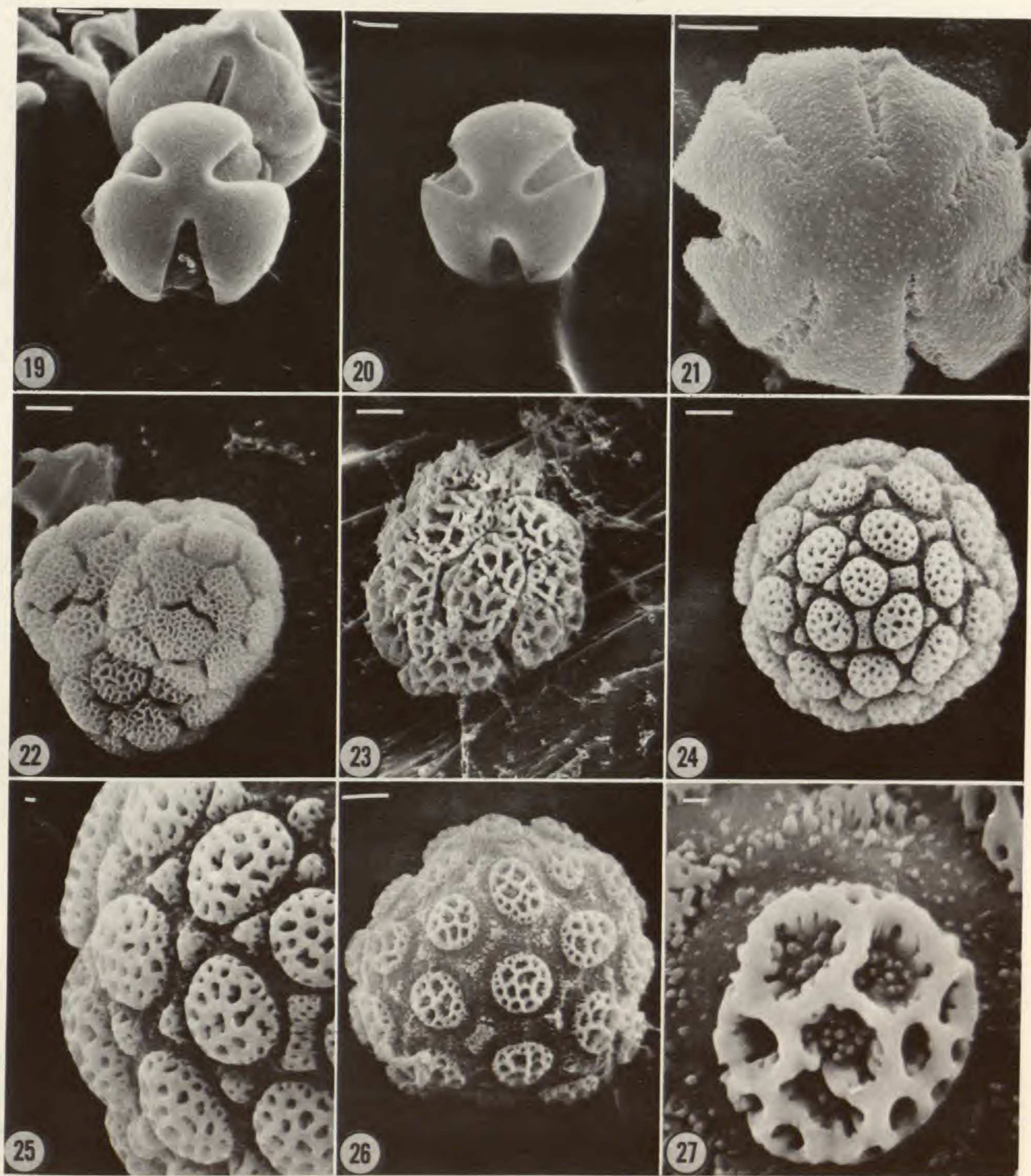
## 3-COLPATE, PSILATE

The closely related but otherwise very isolated South American genera with elongated staminodes—*Jacaranda* (Fig. 20), centered in central and eastern Brazil, and *Digomphia* (Fig. 19) of Guayana—share an almost psilate, 3-colpate pollen. Thus pollen adds nothing to the rather weak evidence supporting segregation of *Digomphia* but emphasizes the isolation of *Jacaranda* and *Digomphia* from other Tecomeae.

## AREOLATE (MODIFIED PERISYNCOLPATE; CAMPORETICULATE)

The basically north-temperate genera *Catalpa* (Fig. 22) and *Chilopsis* (Fig. 23) have areolate or camporeticulate pollen aggregated into tetrads. Two South American genera—*Sparattosperma* (Fig. 9), a monotypic cerrado and dry forest plant with palmately compound leaves, and *Delostoma* (Figs. 24–27), an Andean genus with simple leaves—have single-grained areolate pollen. At least in the case of *Sparattosperma*, which shares an unusual seed wing of fused hairs with *Catalpa*, a relationship to the north-temperate genus is suggested. Interestingly, in the Old World genus *Stereospermum* areolate pollen occurs along with 3-colpate and inaperturate (possibly also monocolpate) pollen (Ferguson & Santisuk, 1973; Buurman, 1977) proving that these differences are not necessarily taxonomically fundamental ones, at least at the generic level.



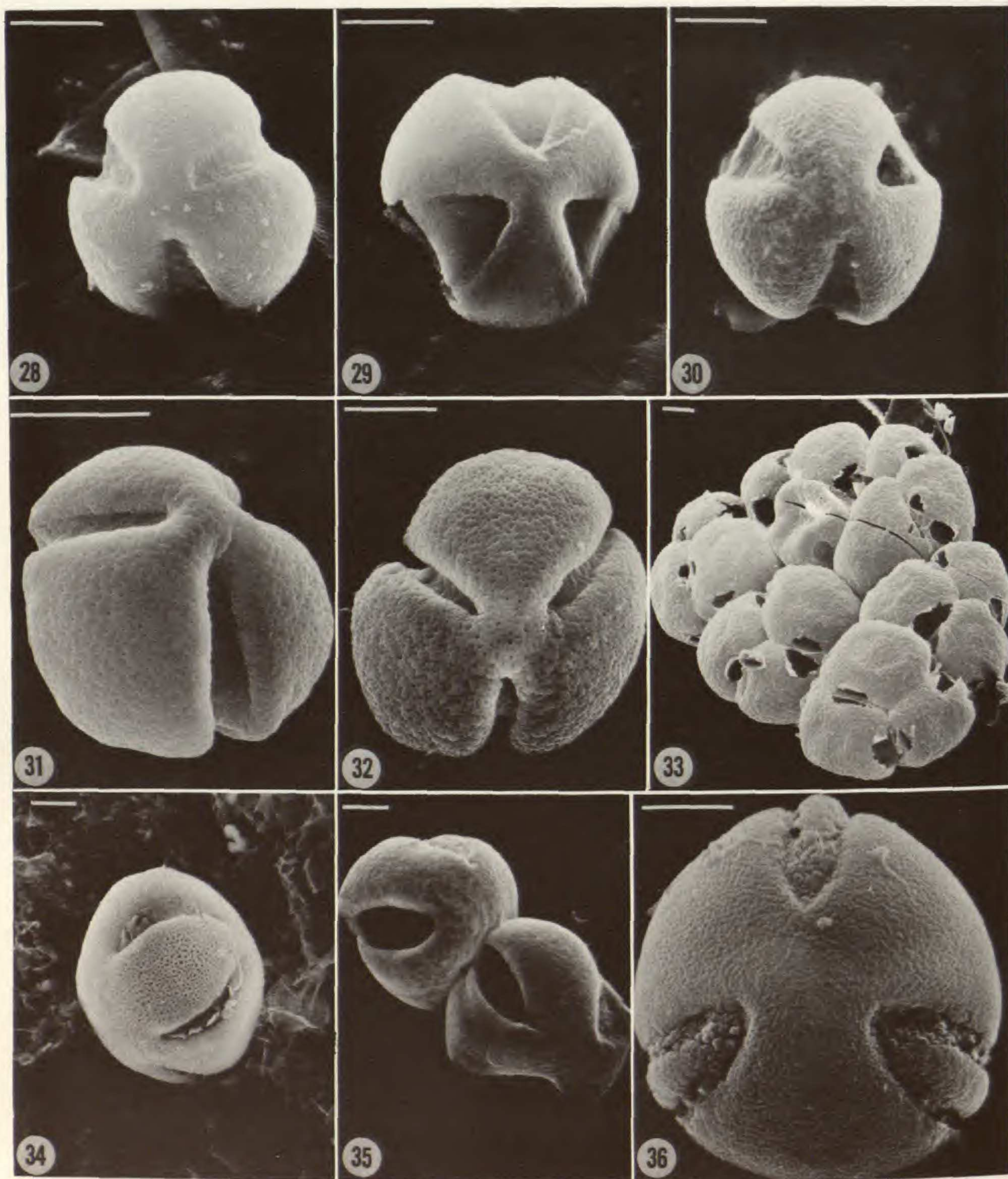


FIGURES 19–27. Palynological variations in Tecomeae—psilate, stephanocolpate, and areolate pollen types.—19. *Digomphia laurifolia*, tricolpate psilate, polar view.—20. *Jacaranda irwinii*, tricolpate psilate, polar view.—21. *Incarvillea emodii*, stephanocolpate, subspinulose.—22. *Catalpa speciosa*, tetrad of areolate grains.—23. *Chilopsis linearis*, tetrad of areolate grains.—24. *Delostoma lobbii*, areolate grain.—25. *Delostoma lobbii*, surface of areolate grain.—26. *Delostoma integrifolium*, areolate grain.—27. *Delostoma integrifolium*, surface of areolate grain. Lines in all figures, except Figs. 25 and 27, equal 10  $\mu$ m. Lines in Figs. 25 and 27 equal 1  $\mu$ m.

#### OROXYLEAE

Four small genera (three monotypic, the fourth with only three species) of southeast Asian trees and nontendrillate climbers with fruit dehiscence parallel to the septum have usually been included in Bignoniaceae. Three of these—*Orox-*





FIGURES 28–36. Pollen types of Tourrettieae, Eccremocarpeae and psilate-foveolate members of Bignoniaceae.—28. *Macfadyena unguis-cati*, polar view.—29. *Arrabidaea chica*, polar view.—30. *Eccremocarpus scaber*, polar view.—31. *Fredericia speciosa*, subpolar view.—32. *Setilobus simplicifolius*, polar view.—33. *Cuspidaria bracteata*, polyad of ca. 24 grains.—34. *Leucocalanthe aromatica*, equatorial view.—35. *Tourrettia lappacea*, polar view. Note loss of colpus exinous material.—36. *Tourrettia lappacea*, polar view. Lines in all figures equal 10  $\mu\text{m}$ .

*ylum* (Fig. 12), *Millingtonia*, and *Hieris*—have the 3-colpate, finely reticulate pollen typical of relatively unspecialized members of most bignon tribes. The fourth, *Nyctocalos*, has unique large (100  $\mu\text{m}$ ), 3-colpate (occasionally varying to pericolpate), strikingly sculptured, very loosely and interruptedly reticulate pollen grains (Ferguson & Santisuk, 1973; Buurman, 1977).



## BIGNONIEAE

The largest and palynologically most diverse tribe of Bignoniaceae, Bignoniaceae are restricted to the neotropics (Gentry, 1979a, 1979b) with a single outlier, *Bignonia capreolata*, in the southeastern United States. The 500 species are mostly lianas and the poorly defined genera are mostly responsible for the bad taxonomic reputation of the family. Palynology has already contributed much to the taxonomy of this tribe (Urban, 1916; Gomes, 1955), and the availability of the SEM provides additional useful information. Seven major palynological categories can be recognized in this tribe, three of them corresponding to the pollen types already listed above for Tecomeae.

## 3-COLPATE, FINELY RETICULATE

A rather diverse group of genera centering around *Pyrostegia* have pollen similar to that characteristic of most Tecomeae. These include *Pyrostegia* (Fig. 3) (1 species in part 4-colpate), *Roentgenia* (ca. 4-colpate) (Figs. 44–45), *Potomogonos*, *Lundia*, *Mussatia*, *Piriadacus*, *Callichlamys*, *Pleonotoma* (including *Nestoria*), *Stizophyllum*, *Pachyptera* (Figs. 17–18) (including *Pseudocalymma*), and *Tanaecium* (but excluding *T. nocturnum* and *T. apiculatum*). These genera are probably not closely related, although their pollen presumably represents an ancestral type shared with most Tecomeae. *Roentgenia* differs somewhat in a tendency to subverrucate sculpturing of the exine.

## 3-COLPATE, PSILATE

Most species of Bignoniaceae have 3-colpate, more or less psilate, usually microperforate, pollen. The following subgroups are recognizable:

(1). Simple tendrils and (usually) pubescent corolla tubes with white to magenta flowers characterize a large group of traditionally recognized genera centering around *Arrabidaea* which share 3-colpate more or less psilate pollen. Many of these genera are monotypic and merger of at least some of them with *Arrabidaea* has been suggested (Gentry, 1977a, 1977b; Sandwith, 1968). Besides *Arrabidaea* (Fig. 29) (including *Cremastus*, *Petastoma*, *Scobinaria*, *Neomacfadya*, *Paramansoa*, etc.), these genera include *Xylophragma* (Fig. 1) (including *Orthotheca*, see Gentry, following paper), *Fridericia* (Fig. 31), *Setilobus* (Fig. 32) (listed as stephanocolpate by Buurman), *Pseudocatalpa*, and *Cuspidaria* (Fig. 2) (including *Saldanhaea* and *Blepharitheca*). *Cuspidaria* differs from the others in pollen aggregated into tetrads, unique in Bignoniaceae. One species, *C. bracteata* (Fig. 33), has polyads, previously unreported in the family and making Bignoniaceae the eighth known polyad-containing angiosperm family (cf. Walker & Doyle, 1975).

(2). A number of small genera with more or less psilate 3(–4)–colpate pollen, pubescent corolla tubes and (2–)3(–multi)–fid (but never unicate, sometimes in part undivided) tendrils form a probably natural group. These include *Periarabidaea*, *Leucocalanthe* (4–5-colpate) (Fig. 34), *Spathicalyx* [including “*Arrabidaea*” *xanthophylla* (Gentry, 1977c)], *Manaosella*, *Ceratophytum*, *Tynnanthus*, and *Paragonia* (including *Sanhilaria*).

(3). Genera with unicate “cat’s claw” tendrils and glabrous corolla tubes make



up a third group, centering around *Macfadyena*, with psilate 3-colpate pollen (Fig. 28). These include *Macfadyena* (including *Doxantha*), *Melloa*, *Dolichandra*, *Parabignonia* (one of the two species with minutely puberulous upper corolla tube), and *Paradolichandra*. Inclusion here of the last three genera, traditionally included in Tecomeae because their capsule dehiscence is (supposedly) perpendicular to the septum, is noteworthy. Morphologically they are very close to the *Macfadyena* alliance and completely out of place in Tecomeae. That their pollen is the same as in morphologically similar *Macfadyena*, but matched in Tecomeae only by utterly different *Jacaranda* and *Digomphia*, supports their placement in Bignoniaceae. Moreover, only *Dolichandra* has fruit dehiscence consistently perpendicular to the septum and even here some fruits are 4-valved and thus both perpendicular and parallel to the septum.

### 3-COLPATE, COARSE-RETICULATE

Only the single genus *Martinella* (Fig. 4) is known to have this type of pollen.

### STEPHANOCOLPATE (ZONOCOLPATE), COARSE-RETICULATE

A natural group of small, closely related genera centering around *Amphilophium*—*Amphilophium* (Figs. 7–8), *Haplolophium*, *Glaziovia*, *Urbanolophium*—has this distinctive pollen type. All these genera are characterized by a frilly outer calyx margin, unique in the family. A few species of *Anemopaegma*, notably *A. insculptum* and *A. robustum*, are stephanocolpate and have a relatively coarse reticulum, thus palynologically approaching this group.

### INAPERTURATE, COARSE-RETICULATE

There are two probably unrelated groups of genera with inaperturate, coarse-reticulate pollen.

(1). Thick-textured white to purple or red flowers, trifid (–multifid) tendrils, and multi-seriate ovules and seeds characterize a group centering around *Pithecoctenium* (Fig. 54) and including also *Distictella* (Fig. 6) and *Distictis* (including *Phaedranthus*, *Wunschmannia*, *Macrodiscus*, and *Anomoctenium*, Gentry, 1974d). *Neves-armondia* should be reduced to *Pithecoctenium* (see Gentry, following paper).

(2). Medium-textured yellow (rarely white or orangish) flowers, simple tendrils and mostly 2-seriate ovules and seeds characterize an assemblage including *Adenocalymma* (Figs. 48–49), most species of *Memora* (Fig. 46), and two of *Tanaecium*. This is certainly a basically natural group and *Memora* could readily be merged with *Adenocalymma* if the not-always-constant definitive character of pinnately compound versus 3-foliolate or 2-foliolate leaves were neglected. *Tanaecium* may be an artificial assemblage based on independent evolution for hawk-moth pollination but more evidence is needed; *T. apiculatum* may be a hawk-moth pollinated derivative of *Adenocalymma* to judge from its pollen; *T. nocturnum* (*Osmohydrophora*) (Figs. 52–53) differs palynologically from other species assigned here in having noticeable pores though lacking colpi.



## INAPERTURATE MEDIUM-RETICULATE

The genera which lack nectariferous discs and favor "multiple bang" flowering phenologies (Gentry, 1974a, 1974b) mostly have inaperturate, medium-reticulate pollen and apparently constitute a natural group, which includes *Clytostoma* (Figs. 37–38), *Phryganocydia* (Fig. 43), and most species of *Cydista* (Figs. 5, 39) (including *Levyia*). All have thin magenta (or white) corollas, simple tendrils, and 8–16 phloem arms in cross-section. Three species of *Cydista*—*C. decora*, *C. lilacina*, and *C. diversifolia* (Fig. 40)—have a similar reticulum but are pericarpate and may represent an intermediate stage with related carpate genera. *Cydista aequinoctialis* may be either pericarpate or inaperturate. *Cydista heterophylla* (Figs. 41–42) is inaperturate but has a unique spinulose exine and apparently is palynologically derived but related. *Roentgenia* (Figs. 44–45), which is morphologically very close to *Cydista* (except for the minutely trifid tendrils), has a similar (though more verrucate or scabrate) pollen reticulum but the grains are carpate; its segregation, and that of 3-carpate monotypic *Potomoganos*, is justified mostly by the palynological difference.

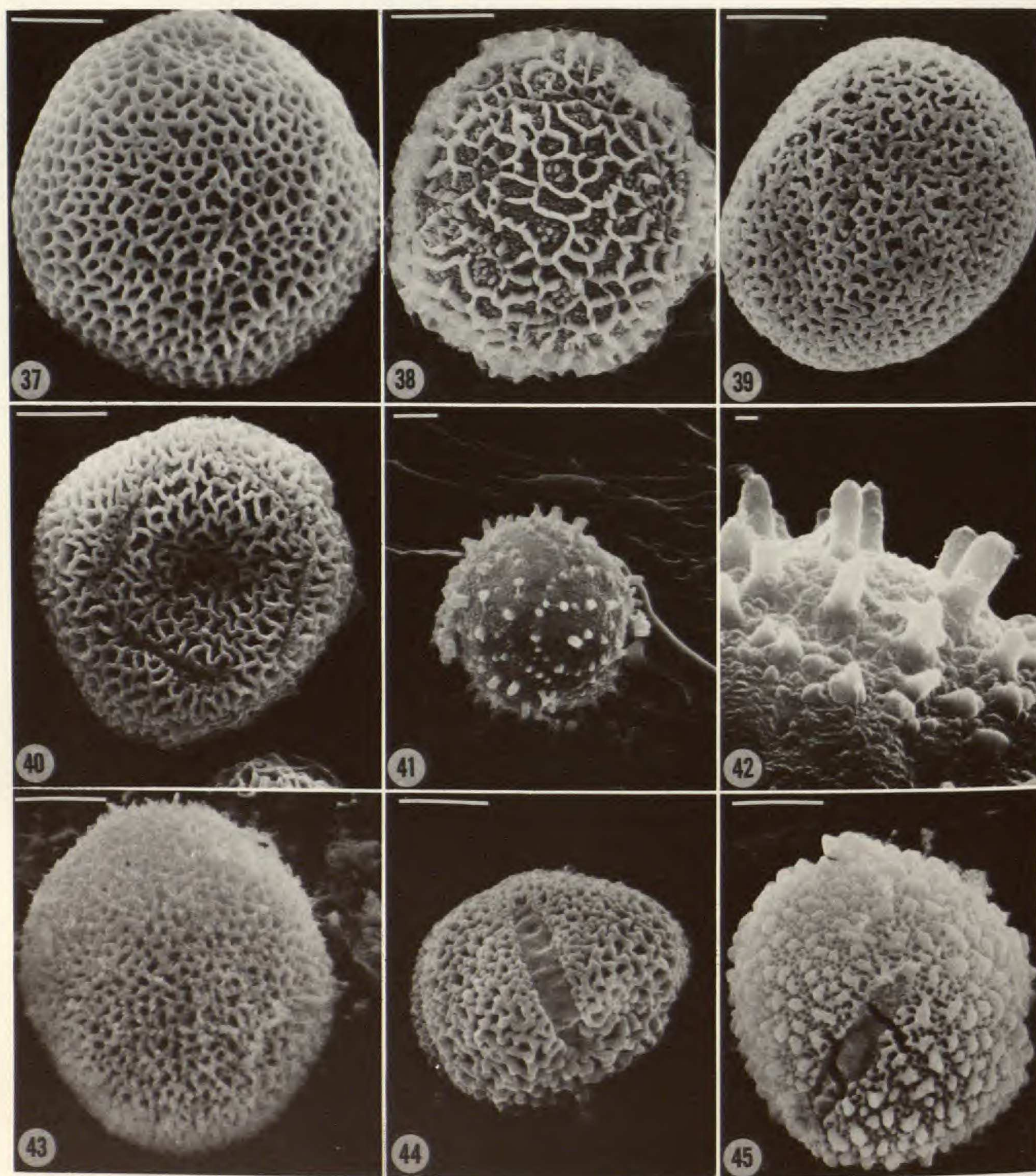
## AREOLATE/PERISYNCARPATE

A number of genera of Bignoniaceae have areolate pollen similar to *Sparattosperma* and *Delostoma* of the Tecomeae. This does not appear to be a natural alliance and consists of at least three distantly related subgroups.

(1). Trifid tendrils and magenta puberulous corollas characterize a natural group of genera, including *Mansoa* and its allies *Gardnerodoxa* and *Onohualcoa*. *Onohualcoa* has already been lumped with *Mansoa*, largely on the basis of the palynological evidence (Gentry, 1976c). *Hanburyophyton* (Fig. 51) should also be reduced to *Mansoa* (see following paper). Interestingly, *Pachyptera alliacea* (Fig. 50) has perisyncarpate pollen (with less pronounced nonreticulate areas) and provides a significant connection between *Mansoa* and the other two onion-smelling species of *Pachyptera* (Fig. 13) which are 3-carpate. These three onion-smelling species are so closely related that Sandwith (1954) considered all three conspecific. *Pachyptera* (Figs. 13, 17–18) is closer to *Mansoa* than to any other genus despite the palynological difference. Three *Cydista* species—*C. diversifolia*, *C. decora*, and *C. lilacina*—also have pericarpate pollen as noted above and may connect mostly inaperturate *Cydista* to the *Mansoa* alliance.

(2). *Anemopaegma* and its allies have cream or yellow flowers with a characteristic shape, trifid or simple tendrils, and a very characteristic stipitate ovary and flattened oblong-stipitate fruit. The pollen of most species is pericarpate to perisyncarpate with the fairly coarse-reticulate exine interrupted by narrow, often interrupted, colpi. The exine of some species of *Anemopaegma* approaches that of *Amphilophium* and its allies but the two groups are not closely related. *Pseudopaegma* was segregated from *Anemopaegma* mainly on account of its 5–6-carpate pollen, whereas *Anemopaegma* was characterized as inaperturate (Urban, 1916). As the SEM makes obvious, the pollen of most species of *Anemopaegma* is actually inconspicuously perisyncarpate, and *Pseudopaegma* should be reduced to synonymy (Gentry, 1976c).

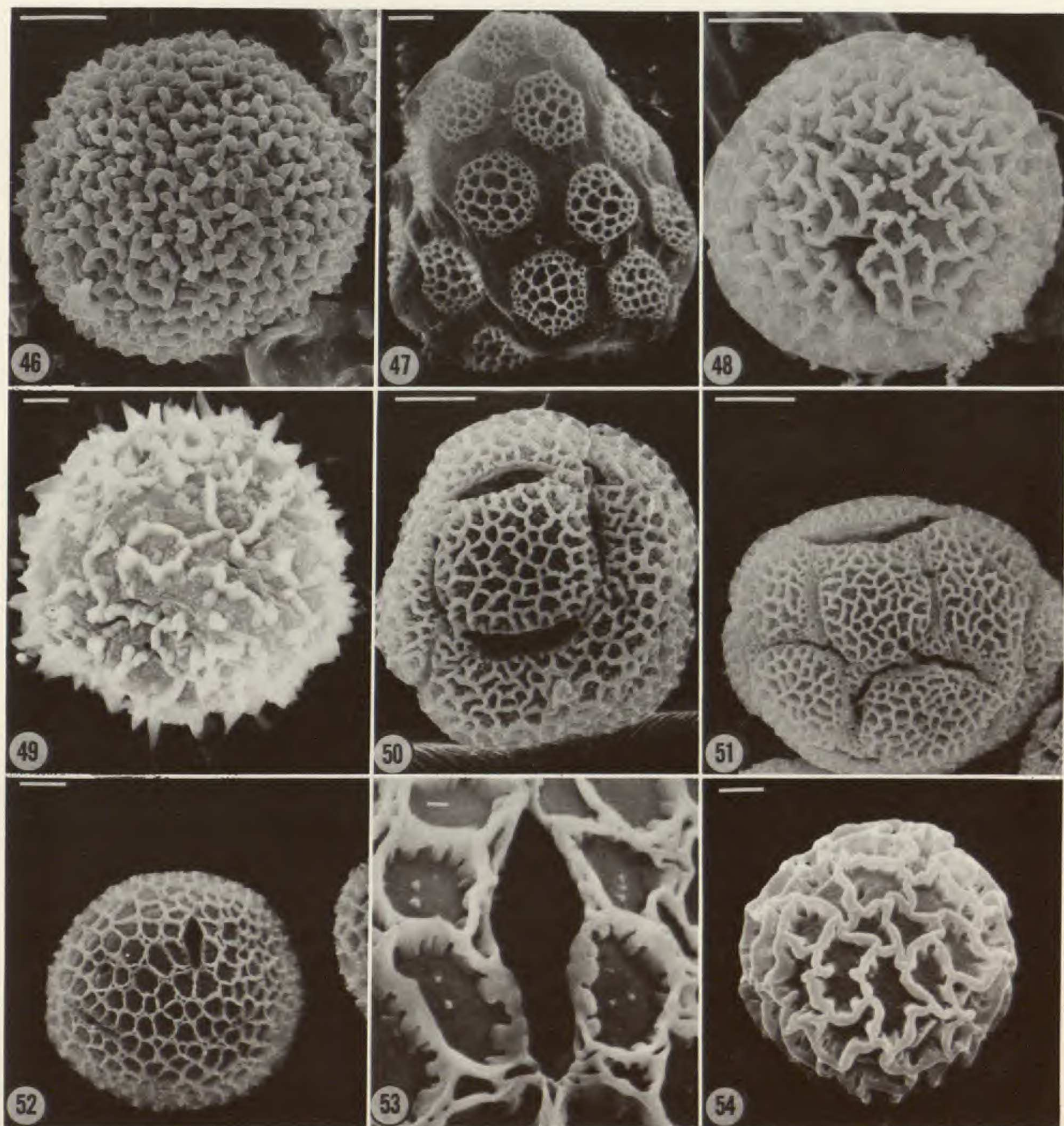




FIGURES 37–45. Intrageneric and intergeneric palynological variations in a natural group of Bignoniaceae—inaperturate, medium-reticulate pollen types and presumably related pollen types of morphologically allied species.—37. *Clytostoma binatum*, inaperturate, medium-reticulate.—38. *Clytostoma uleanum*, inaperturate, coarse-reticulate.—39. *Cydista potosina*, inaperturate, medium-reticulate.—40. *Cydista diversifolia*, pericollate, medium-reticulate.—41. *Cydista heterophylla*, inaperturate, spinulose.—42. *Cydista heterophylla*, exine close up.—43. *Phryganocydia corymbosa*, inaperturate, scabrate.—44. *Roentgenia sordida*, colpate, scabrate.—45. *Roentgenia bracteomana*, colpate, verrucate. Lines in all figures, except Fig. 42, equal 10  $\mu\text{m}$ . Line in Fig. 42 equals 1  $\mu\text{m}$ .

(3). Several species of *Memora*—*M. alba* (Aubl.) Miers, *M. flavida* (DC.) Bur. & K. Schum., *M. pedunculata* (Fig. 47) and several poorly known species from northeastern Brazil—have areolate pollen rather than the continuous exine characteristic of most of the genus. The tendrils are trifid in *M. flavida* and *M. alba*,

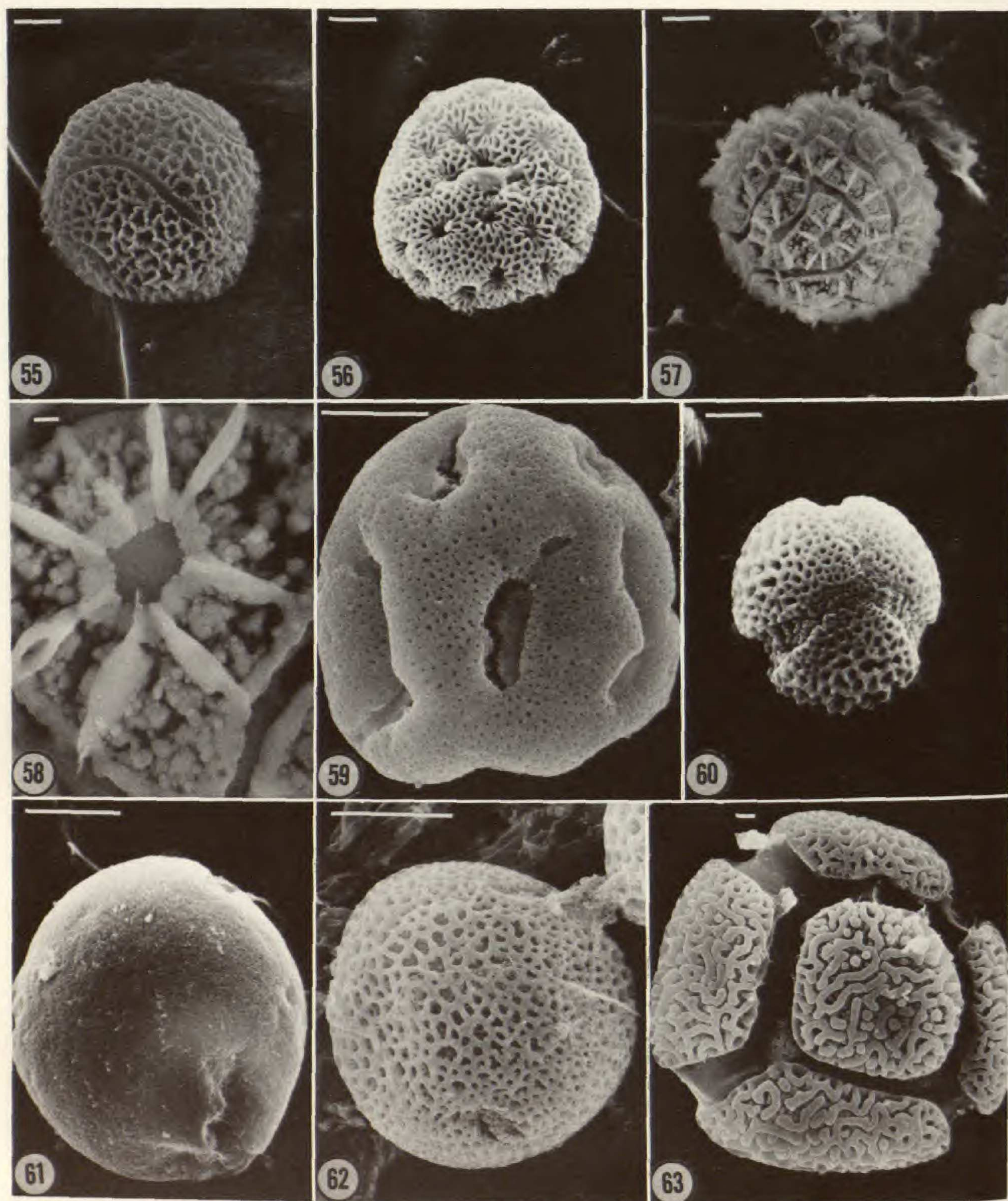




FIGURES 46–54. Palynological variations in Bignoniaceae—coarse-reticulate inaperturate and areolate pollen types.—46. *Memora campicola*.—47. *Memora pedunculata*.—48. *Adenocalymma bracteatum*.—49. *Adenocalymma inundatum*.—50. *Pachyptera alliacea*.—51. *Mansoa lanceolata* (*Hamburyophyton xanthinum*).—52. *Tanaecium nocturnum*.—53. *Tanaecium nocturnum*.—54. *Pithecoctenium crucigerum*. Lines in all figures, except Fig. 53, equal 10  $\mu\text{m}$ . Line in Fig. 53 equals 1  $\mu\text{m}$ .

unique in the genus, but are not known in the other areolate species. These species also have paniculate rather than racemose inflorescences. If the northeastern Brazilian species *M. cristicalyx* A. Gentry and *M. imperatoris-maximilianii* (Wawra) A. Gentry prove to have trifid tendrils, this group might well merit generic recognition. At present, it is best retained as a well-marked section of *Memora*. *Perianthomega vellozoi* (Fig. 63), which is one of the most isolated species of the family, is probably related to this group on account of its areolate pollen and bicomposite leaves.





FIGURES 55–63. Miscellaneous pollen types of neotropical Bignoniaceae.—55. *Neojobertia candolleana* (Bignoniaceae), spiroaperturate.—56. *Macranthisiphon longiflorus* (Bignoniaceae), polyporate, medium-reticulate.—57. *Saritaea magnifica* (Bignoniaceae), polyporate, irregularly spiroaperturate, complexly reticulate.—58. *Saritaea magnifica* (Bignoniaceae), exine close-up.—59. *Amphitecna latifolia* (Crescentieae), polyporate, psilate-foveolate.—60. *Schlegelia nicaraguensis* (Schlegelieae), tri-colpate, medium-reticulate.—61. *Schlegelia fastigiata* (Schlegelieae), triporate, psilate-foveolate.—62. *Schlegelia pandurata* (Schlegelieae), triporate, medium-reticulate.—63. *Perianthomega vellozoi* (Tecomeae?), striate, areolate. Lines in all figures, except Fig. 58, equal 10  $\mu\text{m}$ . Line in Fig. 58 equals 1  $\mu\text{m}$ .



## MISCELLANEOUS

*Neojobertia candolleana* (Fig. 55) has a unique spiroaperturate pollen grain, though sometimes described as areolate (i.e., camporeticulate, Gomes, 1955) or considered operculate-tricolpate (Buurman, 1977). Its unique pollen supports its status as a well-defined monotypic genus.

*Saritaea* (Figs. 57–58) has been widely remarked for its unique, polyporate and irregularly spiroaperturate, complexly reticulate exine with thickened muri radiating out from the apertures and enclosing granular-spinulose, wedge-shaped lumina (Ferguson & Santisuk, 1973; Buurman, 1977). The only remotely similar pollen type in the family is that of *Macranthisiphon* (Fig. 56) which is polyporate with muri radiating out from the pores and enclosing wedge-shaped lumina but a much more regular evenly reticulate sexine. While the palynological evidence strongly supports retention of both these monotypic genera, it also suggests that *Saritaea* might be derived from a *Macranthisiphon*-like ancestor. There is no reason whatsoever to suppose that the complex, highly advanced pollen of *Saritaea* has given rise to the more prevalent, 3-colpate types as suggested by Suryakanta (1973).

## ECCREMOCARPEAE AND TOURRETTIEAE

The pollen of both of these small and isolated monogeneric tribes is psilate and 3-colpate, thus similar to *Jacaranda* and *Digomphia* of the Tecomeae and to many genera of Bignoniaceae. The similarity of pollen between *Eccremocarpus* (Fig. 30) and *Jacaranda* could be interpreted to support Bentham & Hooker's (1876) long discredited treatment of these two genera as belonging to the same tribe but the prevalence of this pollen type in various unrelated groups of Bignoniaceae suggests that it may have little taxonomic significance at the tribal level. *Tourrettia* (Figs. 35–36) is highly anomalous in Bignoniaceae, but its pollen is not out of place, despite the tectate colpi.

## CRESCENTIEAE

This tribe should be restricted to the indehiscent-fruited neotropical species of Bignoniaceae (Gentry, 1976b, 1979b). There are three genera with as many basic pollen types and even intraspecific variation has been reported (Buurman, 1977). *Parmentiera* (Fig. 14) has small-reticulate, 3-colpate pollen similar to that of most species of Tecomeae. *Amphitecna* (Fig. 59) (including *Enallagma* and *Dendrosicus*, Gentry, 1976a) has ecolpate, finely reticulate, multiporate pollen. *Crescentia cujete* has been reported as ecolpate (Urban, 1916) but is actually 6-colpate, having three primary colpi each interrupted equatorially; it is thus palynologically intermediate between *Parmentiera* and *Amphitecna*. *Crescentia alata* with a similar exine to that of *C. cujete* but 3-colpate pollen is not essentially different from *C. cujete*, and its segregation as *Pteromiscus* (Pichon, 1945) is unjustified, even palynologically.

## COLEEAE

The five genera of indehiscent-fruited Madagascar Bignoniaceae (and *Kigelia* of continental Africa) evolved from a different ancestral stock of Tecomeae than



did the neotropical Crescentieae so must be taxonomically separated as tribe Coleeae (Gentry, 1976b). All species which have been examined have the 3-colpate, finely reticulate pollen (e.g., *Ophiocolea*, Fig. 15) typical of unspecialized representatives of most of the other tribes of the family.

### SCHLEGELIEAE

*Schlegelia* and its allies constitute a problematical group intermediate between Bignoniaceae and Scrophulariaceae. As these species have indehiscent, berrylike fruits, they are often placed in Crescentieae but clearly warrant tribal segregation (Gentry, 1979b). Whether Schlegelieae belong in Bignoniaceae or Scrophulariaceae remains unresolved. Symptomatic of the familial problem is the newly described Central American genus *Gibsoniothamnus* (Williams, 1970). Described in Scrophulariaceae to include three species described as Verbenaceae, it was soon discovered that one of these "Verbenaceae" species had previously been described as Bignoniaceae (Gentry, 1971). Specimens of one Panamanian species of *Gibsoniothamnus* were discovered as "indets" referred to five different families (Verbenaceae, Scrophulariaceae, Bignoniaceae, Gentianaceae and Solanaceae) (Gentry, 1974e)! *Schlegelia* itself was described twice, first as Gesneriaceae (later transferred to Bignoniaceae) and then as *Dermatocalyx* of Scrophulariaceae; that these two genera are identical was not discovered until 1949. Another *Schlegelia* species was recently discovered to belong in Boraginaceae (Gentry, 1973).

Pollen of *Schlegelia* (Figs. 60–62) and its relatives is somewhat heterogeneous but of two main types. The large-flowered species of *Schlegelia* [*S. nicaraguensis* (Fig. 60), *S. dressleri*] have 3-colpate, finely reticulate pollen similar to that of most Tecomeae and many Bignonieae but with apparently operculate colpi. Small-flowered species of *Schlegelia* have ecolpate, 3-porate pollen with either a psilate (*S. fastigiata*, Fig. 61) or medium-reticulate (*S. pandurata*, Fig. 62) exine. This palynological dichotomy supports the suggestion (Gentry, 1974c) that *Schlegelia* may constitute two genera, the large-flowered species assignable to Bignoniaceae and the small-flowered ones possibly belonging to Scrophulariaceae. *Gibsoniothamnus* has subpsilate 3-colpate pollen with short colpi and might thus be interpreted as palynologically intermediate between the subpsilate 3-porate species of *Schlegelia* and the more widespread psilate 3-colpate pollen type.

### CONCLUSIONS

Although pollen of Bignoniaceae is indeed heterogeneous, most of the pollen types of the family have evolved independently in several evolutionary lineages, suggesting that these palynological differences may be less fundamental than often supposed. For example, areolate pollen occurs independently in tribes Tecomeae and Bignonieae and repeatedly in unrelated groups within each tribe. Inaperturate pollen has also evolved in several unrelated genera and in both major tribes, and tetrads occur in both major tribes.

Nevertheless, palynological differences are taxonomically very important if correctly interpreted, and most genera are characterized by a single pollen type. We may generalize that certain kinds of intrageneric palynological variation are



allowable, although even the most eurpalynous genera show a single well-developed palynological trend. Thus the change from 3-colpate to perisyncolpate to multiporate to inaperturate in *Tanaecium* (Tomb & Gentry, in prep.) reflects a single evolutionary theme. In *Cydista* the trend is from perisyncolpate to inaperturate with one species—*C. heterophylla*—losing most of its exine reticulation as well as becoming rather spinulose. In the *Pachyptera/Mansoa* alliance we have 3-colpate species in *Pachyptera* and areolate species in *Mansoa* but perisyncolpate *P. alliacea* is intermediate. Reduction of sculpturing of the exine to an irregular, more or less spinulose texture has happened repeatedly in unrelated genera and appears of little taxonomic significance above the species level. On the other hand, the size of exine reticulation appears more conservative than number and type of colpi and is very useful in generic definition. The only genus with significant variation in exine reticulation size is *Clytostoma*, which is uniformly inaperturate but varies from medium reticulate to coarsely reticulate.

The finely reticulate, 3-colpate type of pollen is almost certainly the ancestral or basal type in the family. This can be inferred both from its broad distribution across all tribes and in all geographic regions and from its prevalence in each tribe in taxa regarded as less specialized on morphological grounds. Moreover, in the context of the family as a whole this putatively unspecialized pollen type is most common in the morphologically less advanced Tecomeae and Oroxyleae. The interpretation of finely reticulate, 3-colpate pollen as primitive in Bignoniaceae is in broad agreement with the conclusions of Buurman (1977). However, her additional suggestion that within the 3-colpate palynological group, the smooth-exined *Arrabidaea* type gives rise to the finely reticulate *Tecoma* type is not supported, since the former is restricted to several largely unrelated groups of the specialized tribe Bignonieae and the highly derived genus *Jacaranda* (and its segregate *Digomphia*) in Tecomeae. It seems far more likely that opposite trends toward psilate and coarsely reticulate exines both originated from similar finely reticulate ancestral types.

This survey of Bignoniaceae pollen confirms its taxonomic importance in generic delimitation and suggests that pollen may be equally useful for grouping related genera at the subtribal level. On the other hand, pollen is of minimal taxonomic use at the tribal and familial level in Bignoniaceae. The genera and informal generic groupings proposed here are consistent with all available evidence, palynological as well as morphological, and mostly constitute unarguably natural groups. That the very palynological data which previously have been used to support excessive generic splitting have proven to support larger natural genera and generic groupings is particularly gratifying.

#### LITERATURE CITED

- AIRY SHAW, H. K. 1966. J. C. Willis. A Dictionary of the Flowering Plants and Ferns. Ed. 7. Cambridge Univ. Press, Cambridge.
- BENTHAM, G. & J. D. HOOKER. 1876. Bignoniaceae. *Genera Plantarum* 2(2): 1026–1053.
- BUREAU, E. & K. SCHUMANN. 1896–1897. Bignoniaceae. In Martius, *Flora Brasiliensis* 8(2): 1–452.
- BUURMAN, J. 1977. Contribution to the pollenmorphology of the Bignoniaceae with special reference to the tricolpate type. *Pollen & Spores* 19: 447–519.
- FERGUSON, I. K. & T. SANTISUK. 1973. Notes on the pollen morphology of some Asiatic Bignoniaceae. *Kew Bull.* 28: 187–194.



- GENTRY, A. H. 1971. Note on *Gibsoniothamnus*. *Fieldiana, Bot.* 34: 55.
- . 1973. Generic delimitations of Central American Bignoniaceae. *Brittonia* 25: 226–242.
- . 1974a. Flowering phenology and diversity in tropical Bignoniaceae. *Biotropica* 6: 64–68.
- . 1974b. Coevolutionary patterns in Central American Bignoniaceae. *Ann. Missouri Bot. Gard.* 61: 728–759.
- . 1974c. Bignoniaceae. In *Flora of Panama*. *Ann. Missouri Bot. Gard.* 60: 781–977.
- . 1974d. Studies of Bignoniaceae 11: A synopsis of the genus *Distictis*. *Ann. Missouri Bot. Gard.* 61: 494–501.
- . 1974e. *Gibsoniothamnus* (Scrophulariaceae) in Panama. *Ann. Missouri Bot. Gard.* 61: 533–537.
- . 1976a. *Amphitecna-Enallagma-Dendrosicus* revisited. *Taxon* 24: 108.
- . 1976b. Relationships of the Madagascar Bignoniaceae: a striking case of convergent evolution. *Pl. Syst. Evol.* 126: 255–266.
- . 1976c. Studies in Bignoniaceae 19: Generic mergers and new species of South American Bignoniaceae. *Ann. Missouri Bot. Gard.* 63: 46–80.
- . 1977a. Notes on Middle American Bignoniaceae. *Rhodora* 79: 430–44.
- . 1977b. New species of Leguminosae, Lauraceae, and Monimiaceae, and new combinations in Bignoniaceae from western Ecuador. *Selbyana* 2: 39–45.
- . 1977c. Studies in Bignoniaceae 26: New taxa and combinations in northwestern South American Bignoniaceae. *Phytologia* 34: 183–198.
- . 1979a. Distribution patterns of neotropical Bignoniaceae: Some phytogeographical implications. Pp. 339–354, in K. Larsen & L. Holm-Nielsen, *Tropical Ecology*. Academic Press, New York.
- . 1979b. Bignoniaceae. Part 1: Crescentieae. *Flora Neotropica Monograph* No. 25. (in press)
- GLEISNER, G. & M. RICARDI. 1969. Revision del genero *Argylia* (Bignoniaceae). *Gayana* 19: 1–62.
- GOMES, J. C., JR. 1955. Contribuição a sistemática das Bignoniaceae Brasileiras. *Arq. Serv. Florest.* 9: 261–296.
- LAWRENCE, G. H. M. 1951. *Taxonomy of Vascular Plants*. The Macmillan Co., New York.
- MATTOS, J. R. 1970. *Handroanthus*, um novo genero para os “ipes” do Brasil. *Loefgrenia* 50: 1–4.
- MITRA, K. 1968. Pollen morphology in Bignoniaceae in relation to taxonomy. *Bull. Bot. Surv. India* 10: 319–326.
- PICHON, M. 1945. Notes sur les Bignoniacées. *Bull. Soc. Bot. France* 92: 222–229.
- RENDLE, A. B. 1925. *The Classification of Flowering Plants*. Vol. 2. Dicotyledons. The University Press, Cambridge.
- SANDWICH, N. Y. 1954. Contributions to the flora of Tropical America: LVI. Further studies in Bignoniaceae. *Kew Bull.* 1953: 451–484.
- . 1968. Contributions to the Flora of Tropical America: LXXVI. Notes on Bignoniaceae: XXIX: *Arrabidaea* in Martius's *Flora Brasiliensis* and subsequently. *Kew Bull.* 22: 403–420.
- STANDLEY, P. C. & L. O. WILLIAMS. 1974. Bignoniaceae. In *Flora of Guatemala* X. *Fieldiana, Bot.* 24: 153–232.
- SURYAKANTA. 1973. Pollen morphological studies in the Bignoniaceae. *J. Palynol.* 9: 45–82.
- TOMB, A. S. & A. H. GENTRY. In preparation. Pollen morphology and detailed structure of the Bignoniaceae.
- URBAN, I. 1916. Über Ranken und Pollen der Bignoniaceae. *Ber. Deutsch. Bot. Ges.* 34: 723–758.
- WALKER, J. W. & J. A. DOYLE. 1975. The bases of angiosperm phylogeny: palynology. *Ann. Missouri Bot. Gard.* 62: 664–723.
- WILLIAMS, L. O. 1970. An overlooked genus of the Scrophulariaceae. *Fieldiana, Bot.* 32: 211–214.



## APPENDIX: Species examined.

<i>Adenocalymma inundatum</i> Mart. ex DC.	Woodson et al. 1578 (MO)
<i>A. bracteatum</i> (Cham.) DC.	Williams 7391 (MO)
<i>Amphilophium paniculatum</i> (L.) H.B.K.	Blum 1258 (MO)
<i>Amphitecna latifolia</i> (Mill.) A. Gentry	Dwyer 1568 (MO)
<i>A. sessilifolia</i> (Donn. Sm.) L. Wms.	Wilbur & Stone 9867 (MO)
<i>A. megalophylla</i> (Donn. Sm.) A. Gentry	Wilson 274 (F)
<i>A. montana</i> L. Wms.	Breedlove 25718 (MO)
<i>Anemopaegma arvense</i> (Vell.) Stellf. ex de Souza	Hatschbach 27921 (MO)
<i>A. chrysoleucum</i> (H.B.K.) Sandw.	Gentry 3848 (MO)
<i>A. insculptum</i> (Sandw.) A. Gentry	Prance et al. 14704 (MO)
<i>A. alatum</i> A. Gentry	Steyermark et al. 107753 (MO)
<i>A. orbiculatum</i> (Jacq.) DC.	Gentry 2820 (MO)
<i>A. robustum</i> Bur. & K. Schum.	de la Cruz 3000 (MO)
<i>Argylia potentillaefolia</i> DC.	Wagenknecht 18582 (MO)
<i>A. robusta</i> Sandw.	Senn 4343 (MO)
<i>Arrabidaea bilabiata</i> (Sprague) Sandw.	Lleras et al. P17164 (MO)
<i>A. chica</i> (H. & B.) Verl.	Gentry 7766 (MO)
<i>A. elegans</i> (Vell.) A. Gentry	Mello s.n. (RB-43228) (MO)
<i>A. florida</i> DC.	Gentry 1605 (MO)
<i>A. inaequalis</i> (DC. ex Splitg.) K. Schum.	Rutkis 211 (VEN)
<i>A. podopogon</i> (DC.) A. Gentry	Gentry 8056 (MO)
<i>A. prancei</i> A. Gentry	Prance et al. 13757 (MO)
<i>A. sceptrum</i> (Cham.) Sandw.	Irwin et al. 16163 (MO)
<i>A. triplinervia</i> (DC.) Baill. ex Bur.	Prance et al. 14292 (MO)
<i>A. verrucosa</i> (Standl.) A. Gentry	Gentry 7988 (MO)
<i>Astianthus viminalis</i> (H.B.K.) Baill.	Hinton 9972 (MO)
<i>Bignonia capreolata</i> L.	Bush 2270 (MO)
<i>Callichlamys latifolia</i> (L. Rich.) K. Schum.	Gentry 1896 (MO)
<i>Campsidium valdivianum</i> (Phil.) Skottsb.	Werdermann 74 (MO)
<i>Catalpa speciosa</i> (Ward. ex Barney) Engelm.	Palmer 30318 (MO)
<i>Ceratophytum tetragonolobum</i> (Jacq.) Sprague & Sandw.	Tun 993 (MO)
<i>Chilopsis linearis</i> (Cav.) DC.	Eggers s.n. (MO)
<i>Clytostoma binatum</i> (Thunb.) Sandw.	Gentry 5127 (MO)
<i>C. convolvuloides</i> Bur. & K. Schum.	St. Hilaire s.n. (P)
<i>C. costatum</i> Bur. & K. Schum.	Carauta 279 (GUA)
<i>C. pterocalyx</i> Sprague ex Urb.	Gentry et al. 11032 (MO)
<i>C. sciuripabulum</i> Bur. & K. Schum.	Gentry 12513 (MO)
<i>C. uleanum</i> Kränzl.	Chavez 451 (MO)
<i>Crescentia alata</i> H.B.K.	Wilbur & Stone 1768 (MO)
<i>C. cujete</i> L.	Gentry 3690 (MO)
<i>Cuspidaria bracteata</i> Bur. ex Baill.	Glaziou 11225 (P)
<i>C. convoluta</i> (Vell.) A. Gentry	Hassler 4224 (MO)
<i>C. floribunda</i> (DC.) A. Gentry	Irwin et al. 25769 (MO)
<i>Cydistia aequinoctialis</i> (L.) Miers	Gentry & Tyson 5758 (MO);
	Maguire 24700 (MO)
<i>C. decora</i> (S. Moore) A. Gentry	Camp 3812 (MO);
	Hassler 10022a (MO)
<i>C. diversifolia</i> (H.B.K.) Miers	Webster et al. 12722 (MO)
<i>C. heterophylla</i> Seib.	Gentry 4967 (MO)
<i>C. lilacina</i> A. Gentry	Gentry et al. 10673 (MO)
<i>C. potosina</i> (K. Schum. & Loes.) Loes.	Tun 1211 (MO)
<i>Delostoma lobbii</i> Seem.	Hutchinson et al. 6201 (MO)
<i>D. integrifolium</i> D. Don	Woytkowski 7776 (MO)
<i>Digomphia laurifolia</i> Benth.	Cardona 3027 (VEN)
<i>Distictella magnoliifolia</i> (H.B.K.) Sandw.	Prance 13876 (MO)
<i>Distictis buccinatoria</i> (DC.) A. Gentry	Boutin 3317 (MO)
<i>D. granulosa</i> Bur. & K. Schum.	Haught 2209 (MO)
<i>Dolichandra cynanchoides</i> Cham.	Hassler 12548 (MO)
<i>Dolichandrone spathacea</i> (L.f.) K. Schum.	Gillis 11104 (MO)



## APPENDIX: Continued.

- Eccremocarpus scaber* R. & P.  
*Fridericia speciosa* Mart.  
*Gardnerodoxa mirabilis* Sandw.  
*Gibsoniothamnus latidentatus* A. Gentry  
*G. mirificus* A. Gentry  
*Glaziovina bauhinoides* Bur. ex Baill.  
  
*Godmania aesculifolia* (H.B.K.) Standl.  
*Haplophium bracteatum* Cham.  
*Haplophragma adenophyllum* (Wall. ex G. Don) Dop  
*Incarvillea emodii* (Lindl.) Chatterjee  
*Jacaranda caucana* subsp. *sandwithiana* A. Gentry  
*J. irwinii* A. Gentry  
*Kigelia africana* (Lam.) Benth.  
*Leucocalanthe aromatica* Barb. Rodr.  
*Lundia corymbifera* (Vahl) Sandw.  
*Macfadyena uncata* (Andr.) Sprague & Sandw.  
*M. unguis-cati* (L.) A. Gentry  
*Macranthisiphon longiflorus* (Cav.) K. Schum.  
*Manaosella cordifolia* (DC.) A. Gentry  
*Mansoa difficilis* (Cham.) Bur. & K. Schum.  
*M. glaziovii* Bur. & K. Schum.  
*M. lanceolata* (DC.) A. Gentry  
*M. ventricosa* A. Gentry  
*M. verrucifera* (Schlecht.) A. Gentry  
*Martinella obovata* (H.B.K.) Bur. & K. Schum.  
*Melloa quadrivalvis* (Jacq.) A. Gentry  
*Memora bipinnata* (S. Moore) A. Gentry  
*M. campicola* Pilger  
*M. magnifica* (Mart. ex DC.) Bur.  
*M. patula* Miers  
*M. pedunculata* (Vell.) Miers  
  
*Mussatia hyacinthina* (Standl.) Sandw.  
*Neojobertia candolleana* (Mart. ex DC.) Bur.  
*Ophiocolea floribunda* (Boj.) H. Perr.  
*Oroxylum indicum* (L.) Vent.  
*Pachyptera alliacea* (Lam.) A. Gentry  
*P. hymenaea* (DC.) A. Gentry  
  
*P. kerere* (Aubl.) Sandw.  
*P. parvifolia* A. Gentry  
*P. standleyi* (Steyerm.) A. Gentry  
*Parabignonia unguiculata* (Vell.) A. Gentry  
*Paradolichandra chodatii* Hassler  
*Paragonia pyramidata* (L. Rich.) Bur.  
*Paratecoma peroba* (Record) Kuhlm.  
  
*Parmentiera aculeata* (H.B.K.) Seem.  
*P. macrophylla* Standl.  
*Paulownia tomentosa* (Thunb.) Steud.  
*Perianthomega vellozoi* Bur.  
*Periarrabidaea truncata* A. Samp.  
*Phryganocydia corymbosa* (Vent.) Bur. ex K. Schum.  
*Piriadacus erubescens* (Mart. ex DC.) Pichon  
*Pithecoctenium crucigerum* (L.) A. Gentry  
*P. hatschbachii* A. Gentry  
*Pleonotoma albiflora* (Salzm. ex DC.) A. Gentry  
*P. variabilis* (Jacq.) Miers  
*Potomoganos microcalyx* (G. Mey.) Sandw.
- Boelcke* 6474 (MO)  
*Gottsberger* 788 (MO)  
*Castellanos* 25315 (GUA)  
*Dwyer et al.* 7293 (MO)  
*Wiehler s.n.* (MO)  
*Duarte s.n.* (RB-166032) (MO)  
*Allen* 4492 (MO)  
*Sellow s.n.* (US)  
*Gentry* 1446A (MO)  
*Steward* 14637 (MO)  
*Tyson* 3463 (MO)  
*Irwin et al.* 32250 (MO)  
*Gentry* 6053 (MO)  
*Ducke* 239 (MO)  
*Gentry* 5565 (MO)  
*Gentry* 8380 (MO)  
*Croat* 14031 (MO)  
*Dodson & Thien* 1296 (MO)  
*Hatschbach* 31389 (MO)  
*Marunak* 192 (MO)  
*Glaziou* 12991 (P)  
*Miers* 3080 (P)  
*Maguire et al.* 56083 (MO)  
*Gentry* 6527 (MO)  
*Croat* 14105 (MO)  
*Venturi* 9662 (MO)  
*Hatschbach* 36033 (MO)  
*Irwin et al.* 16477 (MO)  
*Gentry* 13164 (MO)  
*Lasser* 4309 (VEN)  
*Anderson et al.* 35210 (MO)  
*Tun* 992 (MO)  
*Castellanos* 25225 (MO)  
*Gentry* 11360 (MO)  
*Saklani s.n.* (MO)  
*Ducke* 22697 (MO)  
*Breedlove* 24138 (MO);  
*Schwacke & Glaziou s.n.* (MO)  
*Gentry* 7687 (MO)  
*Berlin* 828 (MO)  
*Gentry* 10899 (MO)  
*Blanchet s.n.* (P)  
*Fiebrig* 5071 (P)  
*Croat* 8309A (MO)  
*Evangeliste s.n.* (RB-68377) (RB)  
*Pringle* 7524 (MO)  
*Lewis et al.* 1780 (MO)  
*Allard* 6549 (MO)  
*Hassler* 7356 (US)  
*Gentry* 12824 (MO)  
*Duke* 8781 (MO)  
*Belem* 3617 (MO)  
*Croat* 5804 (MO)  
*Glaziou* 12972 (P)  
*Riedel* 750 (P)  
*Croat* 5607 (MO)  
*Maguire et al.* 29973 (VEN)



## APPENDIX: Continued.

---

<i>Pseudocatalpa caudiculata</i> (Standl.) A. Gentry	Gentry 7662 (MO)
<i>Pyrostegia dichotoma</i> Miers ex K. Schum.	Woytkowski 35089 (MO)
<i>P. venusta</i> (Ker.) Miers	Dusen 15238 (MO)
<i>Rhigozum obovatum</i> Burchell	Gillett 17487 (MO)
<i>Roentgenia bracteomana</i> (Schum. ex Sprague) Urb.	Mexia 6320 (MO)
<i>R. sordida</i> (Bur. & K. Schum.) Sprague & Sandw.	Marcano 199 (VEN)
<i>Saritaea magnifica</i> (Sprague ex v. Steen.) Dugand	Gentry 6049 (MO)
<i>Schlegelia brachyantha</i> Griseb.	Wagner 972 (MO)
<i>S. dressleri</i> A. Gentry	Dressler 3507 (MO)
<i>S. fastigiata</i> Schery	Porter et al. 4432 (MO)
<i>S. nicaraguensis</i> Standl.	Lewis et al. 2319 (MO)
<i>S. pandurata</i> (Moldenke) A. Gentry	Romero C. 5377 (COL)
<i>S. paraensis</i> Ducke	Ducke s.n. (RB-17700) (MO)
<i>S. parasitica</i> (Sw.) Miers ex Griseb.	Burch & Proctor 7117 (MO)
<i>S. parviflora</i> (Oerst.) Monachino	Gentry 17806 (MO)
<i>S. violacea</i> (Aubl.) Griseb.	Mori et al. 8018 (MO)
<i>Setilobus simplicifolius</i> K. Schum.	Guedes 512 (US)
<i>Sparattosperma leucanthum</i> (Vell.) K. Schum.	Seibert 1898 (MO)
<i>Spathicalyx duckei</i> (A. Samp.) A. Gentry	Ducke 17137 (MO)
<i>S. xanthophylla</i> (DC.) A. Gentry	Klug 3410 (MO)
<i>Spathodea campanulata</i> Beauv.	Croat 8890 (MO)
<i>Stizophyllum riparium</i> (H.B.K.) Sandw.	Gentry 7603 (MO)
<i>Tabebuia donnell-smithii</i> Rose	Harmon & Fuentes 5258 (MO)
<i>T. rigida</i> Urb.	Otero 658 (MO)
<i>T. rosea</i> (Bertol.) DC.	Gentry 4579 (MO)
<i>T. stenocalyx</i> Sprague & Stapf	Steyermark 93076 (VEN)
<i>Tanaecium apiculatum</i> A. Gentry	F. Smith 226 (US)
<i>T. crucigerum</i> Seem.	Aristeguieta 5514 (VEN)
<i>T. jaroba</i> Sw.	Hassler 7384 (P)
<i>T. nocturnum</i> (Barb. Rodr.) Bur. & K. Schum.	Bristan s.n. (MO)
<i>Tecoma garrocha</i> Hieron.	Jørgensen 995 (MO)
<i>T. stans</i> (L.) Juss. ex H.B.K.	Sanchez 9 (MO)
<i>Tecomaria capensis</i> (Thunb.) Spach	Bayliss 1748 (MO)
<i>Tourrettia lappacea</i> (L'Her.) Willd.	Davidse & Pohl 1689 (MO)
<i>Tynanthus guatemalensis</i> Donn. Sm.	Gentry 7661 (MO)
<i>Urbanolophium dusenianum</i> (Kränzl.) Melch.	Dusén 16997 (MO);
	Reitz & Klein 4069 (US)
<i>Xylophragma heterocalyx</i> (Bur. & K. Schum.) A. Gentry	Glaziou 14109 (P)
<i>X. seemannianum</i> (O. Ktze.) Sandw.	Gentry 4975 (MO)

---